

Evaluating the "Dual Selection" Hypothesis of Canine Reduction

J. MICHAEL PLAVCAN AND JAY KELLEY

New York College of Osteopathic Medicine, Old Westbury, New York 11568 (J.M.P.); Department of Oral Biology, College of Dentistry, University of Illinois, Chicago, Illinois 60612 (J.K.)

KEY WORDS Canine teeth, Primates, Sexual dimorphism, Anthropoids

ABSTRACT A recently proposed model for canine reduction in hominid evolution (the "dual selection" model) suggests that canine reduction occurs as a result of selection for incorporation of the canines into a functional incisal field. Among the evidence used to support this model are patterns of wear and occlusion of the canine teeth, particularly in female anthropoid primates. We examined wear and occlusal patterns of the canine teeth of 311 male and female anthropoid primates. We find no evidence that the canines are typically occluded tip-to-tip, or that they show wear patterns indicating a "gripping and pulling" function during food ingestion and processing. Furthermore, we do not find compelling evidence that the development of the mesial cristid is associated with canine reduction. While we agree that the mechanisms of selective pressures underlying canine reduction need to be investigated, the "dual selection" hypothesis is unsupported by comparative data.

© 1996 Wiley-Liss, Inc.

Recent studies of canine dimorphism and relative canine tooth size in primates have helped to clarify the factors governing the development and maintenance of large canine teeth (Greenfield, 1992c; Harvey et al., 1978; Kay et al., 1988; Leutenegger, 1982; Leutenegger and Kelly, 1977; Plavcan, 1993; Plavcan and van Schaik, 1992; Plavcan et al., 1995). However, canine tooth size is clearly reduced in a number of lineages, including that of hominids, and these models do not address the mechanisms of canine reduction. Numerous hypotheses have been advanced to explain canine reduction, but, as recently reviewed by Greenfield (1992b, to which we refer the reader for an excellent review of this topic), none receives much support from comparative or developmental evidence in primates. Recognizing this substantial gap in our understanding of canine evolution, Greenfield (1992a,b) recently presented evidence that female canine tooth size and morphology result from selection for functional use as incisors, then generalized

this evidence to the canine teeth of both sexes to formulate the "dual selection hypothesis" of canine reduction in primates. Greenfield has made a number of interesting observations in support of this model. Here, we first review the essential components of the dual selection hypothesis and the evidence used to support it, then critically review this evidence in light of our own observations and those of others.

In brief, Greenfield (1992b) argues that most male canine teeth are large because males compete for access to females, resulting in selection for large canines that function as weapons (Greenfield, 1992c; Kay et al., 1988; Plavcan, 1990, 1993; Plavcan and van Schaik, 1992; Plavcan et al., 1995). However, Greenfield also suggests that the proximity of the canines to the incisors re-

Received December 9, 1994; accepted August 31, 1995.

Address reprint requests to J. Michael Plavcan, New York College of Osteopathic Medicine, Old Westbury, NY 11568.

sults in *simultaneous* selection pressure for their use as incisors in both males and females. This selection pressure favors canine reduction and changes in canine morphology that enhance the functional occlusion between the canines and the adjacent incisors. Putting these ideas together, Greenfield suggests that selection for the use of canines as weapons normally overwhelms selection for the use of canines as incisors in males, but when selection for the use of canines as weapons is relaxed—as in most females and the males of a few species—selection for the use of canines as incisors produces canine reduction and associated morphological changes. Thus, according to this hypothesis, the primary function of the canine teeth in females of most primates is for food procurement, and female canine morphology is accordingly modified to reflect this function. The implication of this hypothesis for human evolution is that, at some time in our ancestry, males, like the females of most other species, stopped using the canines as weapons, and subsequently the canines were incorporated into the incisal functional field.

Greenfield supports the “dual selection” hypothesis with several lines of comparative evidence concerning female canines, including “. . . crown height and projection, occlusal wear, morphology of the crown’s apex, comparative sexual dimorphism in the honing premolar and the maxillary canine, and the interspecific scaling of a variety of crown measurements with each other and body mass.” Of these, the most important lines of evidence that Greenfield marshals to support the canine-as-incisor hypothesis are (1) the presence of blunting apical wear on the tips of both maxillary and mandibular canines in females; (2) the development of the mesial cristid of the mandibular canine; and (3) the relatively small size and low-crowned shape of female canine teeth compared to those of males, which is interpreted as indicating that female canines are not selected for use as weapons in intraspecific fighting.

More specifically, Greenfield argues that the presence of blunting wear on the apices of female canines indicates tip-to-tip occlusion between the maxillary and mandibular canines associated with an incisor-like function of gripping and cutting food. Greenfield

also argues that the mesial cristid of the mandibular canine normally occludes with the distal edge of the maxillary lateral incisor, and that in the shorter canines of females a lower slope to the mesial cristid enhances the functional effectiveness of this occlusal relation. This relation between the slope of the mesial cristid and the crown height of the mandibular canine is interpreted as evidence that selection favors crown height reduction in order to enhance the effectiveness of occlusion between the mandibular canine and maxillary lateral incisor. Greenfield lastly argues that female canine “projection” (a specific estimate of canine crown height intended to measure only that portion of the canine crown which projects beyond the occlusal plane) scales with negative allometry against body mass, while the basal dimensions of the female canines scale isometrically. This is interpreted as evidence that selection has reduced female canines so that they are relatively blunt in comparison to the basal dimensions, and also that selection has not favored changes in female canine size or shape in association with use of the canines as weapons. In additional support of this, Greenfield argues that the size of the honing facet of the mandibular P2 (platyrrhines) or P3 (catarrhines) is larger in females than necessary to accommodate the projection of the maxillary canine. Interspecific variation in female canine projection is explained as “correlated response” (Lande, 1980) to variation in male canine size.

All of these lines of evidence are important to the dual selection model, but fundamentally, if female canines are *not* used as incisors, then it is difficult to support the hypothesis that selection favors their development as such, since there is no functional/morphological complex with a fitness consequence to individuals on which selection can act.

MATERIALS AND METHODS

We evaluated evidence for the dual selection hypothesis by examining the canine teeth of 311 specimens of anthropoid primates from the American Museum of Natural History and the Field Museum of Natural History. Three aspects of the canines were

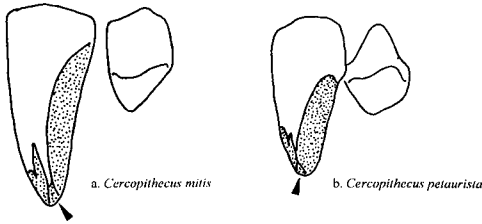


Fig. 1. Camera lucida drawings of female maxillary canines and P3s from two species of *Cercopithecus* showing wear facets formed on the maxillary canines. Each drawing was done at the same magnification and is shown in a lingual view. The mesial and distal facets occur on the mesial and distal edges of the tooth, respectively. A third "beveled" wear facet (arrows) is located at or near the apex of each tooth, between the mesial and distal facets.

evaluated: first, whether the canines could be physically occluded tip-to-tip; second, whether the mesial cristid of the mandibular canine could occlude with the lateral maxillary incisor, and whether there was wear indicating that such contact occurred in life; and third, the presence or absence of wear facets on the maxillary canine.

Canine tip-to-tip occlusion was evaluated by placing the jaws in centric occlusion, then maneuvering the jaws to see if the canines could be occluded tip-to-tip. To render our evaluations conservative (giving the benefit of the doubt to the dual selection hypothesis), we scored occlusion without regard to the presence of soft tissues in the temporomandibular joint. We did not score canines as occluding if the tips could not be brought into contact. Specimens with either one or both postglenoid processes broken were not examined. Where the canines could be occluded tip-to-tip, we looked for evidence of matching wear facets on the apices of the maxillary and mandibular canines. Contact of the mesial cristid with the maxillary lateral incisor was evaluated in a similar fashion.

The presence or absence of three wear facets was scored for each canine tooth: a mesial facet, a distal facet, and a lingually tilted "beveled" facet (Fig. 1). Additionally, where there was evidence of wear at the apex that blunted the tooth, we noted whether such wear presented a horizontal flattened facet, blunting wear that rounded the apex of the

tooth, or wear that occurred after breakage of the tip of the canine. In all cases, we examined the teeth to determine as best as possible which surfaces of the mandibular teeth were likely to produce the wear facets noted on the maxillary canine.

RESULTS AND DISCUSSION

Canine occlusion and wear

Greenfield (1992b) states that "[w]ith respect to crown height, female canines in most anthropoid species are short enough to permit tip-to-tip maxillary canine/mandibular canine and mandibular canine/maxillary lateral incisor contact and observations of occlusal wear confirm that these types of occlusion are common . . ." (p. 161).

In fact, in 47% of the males and 24% of the females that we examined it was possible to occlude the canines tip-to-tip. Among the males, tip-to-tip occlusion was more likely when the canines were virtually unworn. In both the males and females of every species that we examined, tip-to-tip occlusion of the canines required that the lower jaw be retracted, and that the condyle be jammed against the postglenoid process. In life, the presence of vascular and other soft tissue in the tempromandibular joint would probably preclude tip-to-tip occlusion of the canines in most specimens that we examined. More importantly, retraction of the mandible is not a typical jaw movement during mastication, and in the majority of the specimens that we examined, the mandible had to be dislocated (moving the condyle posteriorly out of the fossa) to occlude the canines tip-to-tip! Further, while the female canines are usually shorter than those of males, they are usually so tall that occlusion of the other teeth—especially the incisors—is impossible when the canines are positioned tip-to-tip. Therefore, even if the canines did occlude tip-to-tip for food gathering or processing, such occlusion could not occur in concert with occlusion of the incisors.

On the basis of wear patterns we find little evidence that canine tip-to-tip occlusion is either common or important to canine function. Figures 1 and 2 show camera lucida drawings of lingual views of female maxillary canines of several catarrhine species.

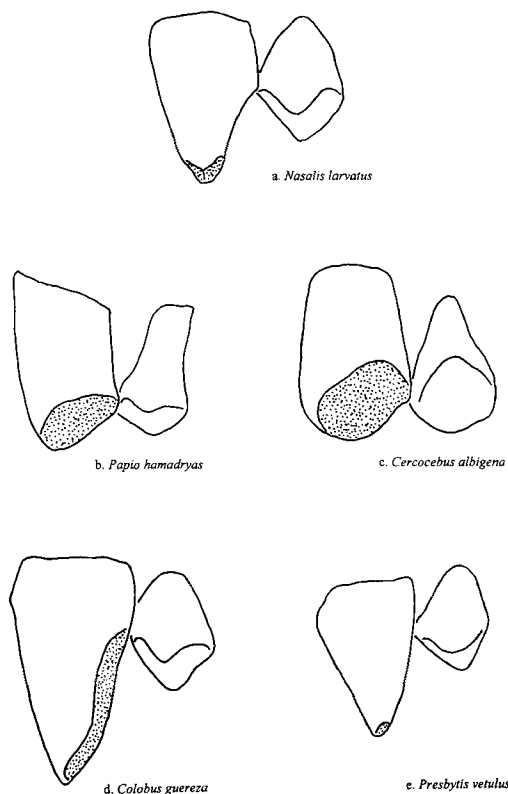


Fig. 2. Camera lucida drawings of female maxillary canines and P3s of several anthropoid species illustrating canine wear facets (stippled). All drawings were done at the same magnification and are shown in a lingual view.

Of the 311 specimens that we examined, we observed no cases of a pattern of canine tip wear that suggests that the canines are occluded tip-to-tip. What we did find is that males and females usually show similar patterns of tooth wear on the maxillary canine, with mesial and distal facets commonly formed, a beveled wear facet sometimes present, and slight apical wear occasionally present.

The maxillary canine of both sexes typically forms a distal wear facet from occlusion with the buccal face of the mandibular P2 (platyrrhines) or P3 (catarrhines). This wear facet begins near the tip (e.g., *Presbytis vetulus*, Fig. 2e) and with age progresses down the distal edge of the tooth. As the individual ages, the canine becomes shorter and the

distal wear facet becomes larger (e.g., *Colobus guereza*, Fig. 2d). With advanced age or severe wear, the facet becomes nearly horizontal (e.g., *Papio hamadryas*, Fig. 2b, and *Cercocebus albigena*, Fig. 2c) as the tooth is worn down to a nub. We observed a distal wear facet on 99% of the males and 97% of the females examined (Table 1).

In 96% of the males and 88% of the females that we examined (Table 1), a mesial wear facet was observed, formed by contact with the distal edge of the mandibular canine (Fig. 1, Fig. 2a). In many species, this wear facet is very poorly developed by comparison to the distal wear facet. Where mesial facets are well developed, contact of the distal and mesial wear facets near the apex gives the canine a chiseled appearance. Even wear that is restricted to the apex of the tooth produces this pattern (e.g., *Nasalis larvatus*, Fig. 2a).

Occasionally there is a third wear facet formed near the apex of the maxillary canine tooth which we refer to as a "beveled" facet (Fig. 1). Where this facet is formed by tooth-to-tooth contact it is not flat and horizontal (as might be expected by habitual tip-to-tip contact), but rather beveled toward the lingual side of the tooth. In no case was there a matching wear facet present on the apex of the mandibular canine that indicated formation of the facet through tip-to-tip contact between the canines. We regard the most likely mechanism forming this wear facet as contact with the embrasure formed by the meeting of the distal heel of the mandibular canine with the adjacent mandibular premolar. We observed this type of wear on 30% of the males and 19% of the females that we examined (Table 1).

Occasionally, the tips of the canines are slightly rounded by wear. Where the enamel is thin and apical wear is advanced, the wear exposes the underlying dentin, forming a small ring of enamel surrounding a small dentin "lake" like those seen on the tips of the postcanine tooth cusps. We observed this wear in approximately 25% of the individuals examined, but it was not clearly expressed in any of the cercopithecoids. Most importantly, there is typically no indication of a flattened facet as expected by habitual contact between two opposing tooth sur-

TABLE 1. Listing of observed incidences of wear facets and occlusal relations in males and females

Species	Wear facets				Occlusal relations	
	Distal	Mesial	Bevelled	Apical	Tip-to-tip	/C-I ²
<i>Saimiri sciureus oerstedii</i>						
Males (30)	29	29	10	0	0	30
Females (16)	13	14	0	6	0	16
<i>Lagothrix lagothricha poeppigii</i>						
Males (5)	5	5	3	0	3	5
Females (9)	9	8	1	2	2	9
<i>Ateles geoffroyi vellerosus</i>						
Males (11)	11	11	5	2	3	11
Females (14)	14	14	6	1	1	14
<i>Cebus olivaceus apiculatus</i>						
Males (13)	13	13	2	3	8	13
Females (14)	14	14	4	5	5	14
<i>Alouatta seniculus seniculus</i>						
Males (13)	13	9	1	0	5	13
Females (12)	12	6	0	2	1	12
<i>Pithecia pithecia</i>						
Males (17)	17	15	3	6	13	9
Females (7)	7	7	0	1	4	4
? (6)	6	6	0	3	4	6
<i>Callicebus torquatus lugens</i>						
Males (19)	19	19	0	9	10	19
Females (17)	17	17	0	10	8	17
? (2)	2	2	0	0	2	2
<i>Aotus lemurinus lemurinus</i>						
Males (3)	3	3	2	0	1	3
Females (7)	7	7	0	0	2	7
? (9)	9	9	1	0	4	9
<i>Pan troglodytes schweinfurthii</i>						
Males (8)	8	8	1	3	3	8
Females (1)	1	1	0	0	0	1
<i>Pan troglodytes troglodytes</i>						
Males (3)	3	3	0	0	0	3
Females (1)	1	1	0	0	0	1
<i>Pan troglodytes verus</i>						
Males (1)	1	1	0	0	1	1
Females (2)	1	1	0	0	0	2
<i>Macaca fascicularis</i>						
Males (5)	5	5	2	0	3	4
Females (8)	8	6	3	0	1	3
<i>Macaca nemestrina</i>						
Males (4)	4	4	2	0	4	4
Females (4)	4	4	2	0	2	4
<i>Cercocebus albigena</i>						
Males (3)	3	3	1	0	3	0
Females (5)	5	3	0	0	1	0
<i>Cercopithecus aethiops</i>						
Males (6)	6	6	4	0	5	2
Females (6)	6	4	2	0	2	5
<i>Cercopithecus mitis</i>						
Males (5)	5	5	4	0	3	5
Females (6)	6	6	5	0	2	5
<i>Colobus guereza</i>						
Males (6)	6	6	6	0	4	3
Females (3)	3	2	1	0	2	3
<i>Presbytis hosei</i>						
Males (6)	6	6	2	0	5	3
Females (4)	4	4	2	0	0	4
Totals						
Males (158)	157	151	48	23	74	136
	99%	96%	30%	15%	47%	86%
Females (136)	132	119	26	27	33	121
	97%	88%	19%	20%	24%	89%
? (17)	17	17	1	3	10	9
	100%	100%	6%	18%	59%	53%
All (311)	306	287	75	53	117	266
	98%	92%	24%	17%	38%	86%

faces. In fact, the wear that we observed appears to be analogous to that seen on the tips of the molar cusps, where it is commonly attributed to puncture-crushing (Hiimäe and Kay, 1973). Given that this apical wear is similar to that seen on the cusps of the postcanine teeth, incidental contact with food during food gathering and processing seems to be a sufficient alternative explanation for the presence of slight, blunting apical wear.

Crown morphology

Greenfield (1992a,b) notes that in many females the mandibular canine has a mesial cristid that occludes with the lateral maxillary incisor. Mesial cristid/lateral maxillary incisor contact was possible in 86% of the males and 89% of the females that we observed (Table 1). We agree that this may represent a functional contact between these teeth, but we question the interpretation of this as evidence that female canines primarily function as incisors. That the mandibular canine and maxillary lateral incisor occlude is, of course, a matter of proximity. As Greenfield noted, though, not all individuals of species, or all species for that matter, show such contact, leaving open the question of the function of the mesial cristid in a number of cases.

Greenfield demonstrates that the development of the mesial cristid is proportional to the crown height of the mandibular canine, such that taller-crowned teeth have a more steeply angled cristid. Greenfield hypothesizes that, because of this relation, selection favors a reduction in crown height in order to enhance the development of the mesial cristid. But this seems to be an allometric phenomenon, as noted by Greenfield (1992b). We therefore question whether this demonstrates that the development of the cristid reflects selection for use of the mandibular canine as an incisor. Because the angle of the cristid reflects mandibular canine crown height, it could be just as easily an allometric by-product resulting from changes in crown height, regardless of the selective or non-selective mechanism producing such changes. Because female canines are almost universally lower crowned than those of males, it is to be expected that they will show

a more shallowly angled mesial cristid than males. Deciduous canines are relatively even lower crowned and, as expected, tend to have even more shallowly sloped mesial cristids (Greenfield, 1992b).

It is important to note that the mesial cristid is only one morphological feature of the mandibular canine, and the discussion of this feature leaves open the question of why maxillary canine teeth in females do not look like incisors. Greenfield argues that, unlike that of male canines, female maxillary canine "projection" scales with negative allometry, while female occlusal canine dimensions scale isometrically against body mass. This is interpreted as indicating that selective forces do not alter female canine form for more efficient use as weapons. However, Greenfield's measure of canine "projection" is subject to a number of artifactual errors (Plavcan, 1993), including variation in premolar number, relative postcanine tooth crown height, and variation in the curve of Spee. Using a direct measure, female canine crown height scales with only slight negative allometry (Plavcan, 1990; Plavcan et al., 1995), but this masks substantial variation in the scaling coefficients within taxonomic groups. This suggests that anthropoid-wide scaling coefficients for canine crown height reflect interactions between taxonomy, behavior, and body size (Plavcan, 1993), casting doubt on the strength of inferences that can be gleaned from scaling coefficients alone.

Greenfield further suggests that variation in female crown height may be a function of correlated response to variation in male canine crown height (Lande, 1989). Plavcan et al. (1995) also show that male and female relative canine crown height are correlated, suggesting that correlated response to variation in male canine size may explain some variation in female canine crown height. However, close scrutiny of this relation (Plavcan et al., 1995), coupled with observation of substantial variation in canine dimorphism, shows that if correlated response operates in anthropoid primates, it is only a secondary effect by comparison to selection for the development of canines as weapons in females (see below).

Finally, there is reason to doubt that, even

if there is selection to alter mandibular canine morphology in association with diet, such alterations either necessarily constrain or are constrained by maxillary canine morphology. Strepsirrhines have incorporated the mandibular canine into the tooth comb. In this case, the mandibular canine has clearly been incorporated into the incisal functional field and has been modified to look much like the other incisors, while the mandibular P2 has been modified to look—and presumably function—like a canine. This demonstrates that, at least in strepsirrhines, mandibular canine crown morphology can be substantially altered without concomitant alterations in maxillary canine crown morphology. Still, it is also important to note that in all strepsirrhines male and female canine size are similar, so this argument does not address the hypothesis that female maxillary canine crown morphology in most anthropoids is affected by correlated response.

Canine function

In further support of the dual selection hypothesis, Greenfield makes two important assumptions: first, that female canines are *not* selected for use as weapons, and second, that female canines are used as incisors during feeding. A number of studies document the relations between canine dimorphism, male canine size, and intrasexual competition (Greenfield 1992a; Kay et al., 1988; Plavcan, 1990, 1993; Plavcan and van Schaik, 1992; Plavcan et al., 1995), even though the influence of various other factors, such as phylogenetic inertia, predation pressure, and body size, are still debated. Greenfield suggests that female canines are not selected as weapons, citing Smith's (1981) study that found no relation between female canine size and mating system, as well as a lack of any other evidence that female canine size is related to intrasexual competition. Greenfield further notes that females usually compete for resources rather than mates, but hypothesizes that this should result in little or no selection for the development of weaponry, and even that female canines are possibly of no value as weapons. Greenfield (1992b, p. 168) states that "[e]ven if a systematic study of female anthropoid

behavior shows that they bite with their canines and occasionally engage in fights, the morphology, size, and occlusion of their canine teeth indicate that the *selection* related to these behaviors has relatively little impact on the tooth's design."

More recent studies (Plavcan and van Schaik, 1993; Plavcan et al., 1995) provide evidence that female canines, like male canines, are selected for use as weapons, and that variation in female canine size is strongly linked to estimates of the intensity of female competition (which is not necessarily concordant with traditional classifications of mating system). Plavcan et al. (1995) suggest that females generally have smaller canines than males because females do not compete as intensely as males, because they compete in coalitions (thereby reducing the selective benefits of large canines to individuals), or because the fitness consequences of female competition are generally lower than for males, resulting in less selective pressure to develop hypertrophied canines. It is important to note that even though female canines are usually not as large as those of males, many female primates have canines that are substantial in size and that can inflict serious, even lethal wounds (Gust and Gordan, 1991). In comparing female canines to those of males, it is probably more accurate to say that most male anthropoid primates have extremely hypertrophied canines, rather than that females possess diminutive canines. Thus, Plavcan et al. (1995) agree with Greenfield that agonistic competition between females over resources might result in weaker selection pressure for the development of weaponry than does competition for access to mates, but this is a far cry from asserting that competition for resources results in *no* selection for weaponry.

In contrast to evidence that female primates use their canines as weapons, to our knowledge there is no evidence that female anthropoids as a group habitually use their canines as incisors in food gathering, with the exception of the pithecines and *Cebuella* (noted by Greenfield, 1992c). Both male and female pithecines use their canines to open hard fruit. Greenfield argues, in support of his model, that the occlusion of the maxillary

and mandibular canines in these animals is analogous to that between the mandibular canine and lateral incisors of other anthropoids, but we are at a loss to see how this is so. As Greenfield notes, female pitheciines have large canines with a wide diastema separating the canines from the incisors. This seems to represent a morphological specialization quite different from that discussed by Greenfield for other anthropoids. Furthermore, pitheciines are clearly using their canines to do what their incisors cannot do (open hard objects), demonstrating that use of the canines for food procurement does not necessarily mean that the canines will function as incisors or look like incisors.

Greenfield further suggests that selection for the use of the canines as incisors operates in males as well as females, even though "... the projection, morphology, and usual pattern of wear on most male anthropoid canines do not lead one to suspect that there is selection favoring their use as incisors" (Greenfield, 1992b, p. 161). We emphatically concur with this latter assessment. Consequently, we fail to see how selection for the use of the canines as incisors explains canine reduction in the males of most anthropoid species. In order for selection to modify a structure for a particular function, there must be some variability in function and morphology with an effect on individual fitness on which selection can operate. If male canines are not used as incisors, and in fact *cannot* be used as incisors, how can selection operate for this consequence unless it is somehow prescient of future use?

This point leads finally to Greenfield's evaluation of human canine evolution using the dual selection model. Greenfield argues that canine reduction in human evolution is the consequence of, first, a lack of use of the canines as weapons and, second, selection to incorporate the canines into the incisal functional field. In spite of our critique of Greenfield's model, we agree that human canine reduction is probably associated with a lack of selection for the development and/or maintenance of canines as weapons in both sexes. We furthermore do not disagree with the hypothesis that human canines currently can function in concert with the incisors for food procurement. Rather, following

our discussion above, we question the evidence that selection reduced human canines *specifically* in association with this latter function. We feel that it is important to make clear distinctions between a general model for the selective forces that produce canine reduction in primates, any additional selective forces that might have favored canine reduction specifically in human evolution, and selective forces that may currently operate on human canine size and morphology. For example, it is not unreasonable to hypothesize that once canine reduction occurs (for whatever reason), selection can subsequently modify the canines in association with a new use, not possible before canine reduction. Thus, in human evolution, some as yet unspecified factor might have favored canine reduction following or in concert with relaxed selection to develop or maintain large canines, particularly in males. Following canine reduction, canine crown morphology might have been subsequently altered to enhance their ability to function in concert with the incisors. An alternative explanation is that selection has not modified the canines specifically for use as incisors in humans. The capacity for canines to function with the incisors in food gathering may represent nothing more than a by-product of canine reduction coupled with the juxtaposition of the canines and incisors. In this sense, the use of small canines for food gathering in humans would represent an exaptation, following the definition of Gould and Vrba (1982). In neither of these scenarios is canine reduction associated with any current dietary function of the canines.

In conclusion, the hypothesis that canine morphology and size are influenced by diet is not unusual, and is not necessarily unreasonable. There is strong evidence that selection has altered one or both canines for dietary specializations in a number of species. Pitheciines clearly have canine teeth that are specialized for opening hard objects as reflected by their large size and unusual chisel-like morphology. The mandibular canines of *Cebuella* are clearly altered into incisor-like teeth, and incorporated with the other mandibular incisors into a gouge-like structure that is used to dig holes in tree trunks to extract gums (Greenfield, 1992c). Likewise,

many strepsirrhines have modified the mandibular canine into an incisor-like structure and incorporated it into the tooth-comb. In all of these taxa, the canines are clearly modified from the more typical tall-crowned tooth with a single cusp, and behavioral observations confirm that the canines are used in a specific way. All of this suggests that when canines function as incisors, they are modified by selection to look like incisors in both sexes. The dual selection hypothesis, though, suggests that the canines of all anthropoids—male and female—are under selective pressure to function as incisors. However, in reviewing the arguments for the dual selection hypothesis, we find little compelling evidence that the canines of either males or females are under selective pressure to function as incisors. The morphological evidence put forward by Greenfield to support the hypothesis that female (or male) canine morphology is a response to selection for use as incisors is anatomically impossible under normal conditions in most taxa (tip-to-tip occlusion of the canines), unsubstantiated by examination of the canine teeth of a variety of anthropoids (canine wear patterns), or equally well explained as a nonselected growth phenomenon (mesial cristid/crown height relation).

Understanding the mechanisms underlying canine reduction in primates is clearly important, particularly if such an understanding helps to interpret the evolution of the anterior dentition in hominids. At this point, though, we are aware of no hypothesis that satisfactorily explains canine reduction (as reviewed by Greenfield, 1992b), including the dual selection hypothesis. Thus, while the factors influencing the development and maintenance of large canine teeth in both male and female primates are becoming progressively better understood, the mechanisms underlying canine reduction are still unknown.

ACKNOWLEDGMENTS

We thank Ross MacPhee and Wolfgang Fuchs of the American Museum of Natural

History, and the staff of the Field Museum of Natural History for access to specimens in their care. We thank Matt Cartmill and three anonymous reviewers for their helpful comments which greatly improved the manuscript.

LITERATURE CITED

- Gould SJ, and Vrba ES (1982) Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15.
- Greenfield LO (1992a) A nonadaptive dental trait. *Int. J. Primatol.* 13:631–657.
- Greenfield LO (1992b) Origin of the human canine: A new solution to an old enigma. *Yearb. Phys. Anthropol.* 35:153–185.
- Greenfield LO (1992c) Relative canine size, behavior, and diet in male ceboids. *J. Hum. Evol.* 23:469–480.
- Gust DA, and Gordan TP (1991) Female rank instability in newly formed groups of familiar Sooty Mangabeys (*Cercocebus torquatus atys*). *Primates* 32:465–471.
- Harvey PH, Kavanagh M, and Clutton-Brock TH (1978) Sexual dimorphism in primate teeth. *J. Zool. (Lond.)* 186:474–485.
- Hiimäe KM, and Kay RF (1973) Evolutionary trends in the dynamics of primate mastication. In MR Zingeser (ed.): *Craniofacial Biology of Primates*. Symp. IVth Int. Congr. Primatol., Vol. 3. Basel: Karger, pp. 28–64.
- Kay RF, Plavcan JM, Glander KE, and Wright PC (1988) Sexual selection and canine dimorphism in New World monkeys. *Am. J. Phys. Anthropol.* 77:385–397.
- Lande R (1980) Sexual dimorphism, sexual selection and adaptation in polygenic characteristics. *Evolution* 34:292–307.
- Leutenegger W (1982) Scaling of sexual dimorphism in body weight and canine size in primates. *Folia Primatol.* 37:163–176.
- Leutenegger W, and Kelly JT (1977) Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* 18:117–136.
- Plavcan JM (1990) Sexual Dimorphism in the Dentition of Extant Anthropoid Primates. Ph.D. dissertation, Duke University.
- Plavcan JM (1993) Canine size and shape in male anthropoid primates. *Am. J. Phys. Anthropol.* 92:201–216.
- Plavcan JM, and van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 87:461–477.
- Plavcan JM, and van Schaik CP (1993) Reconsidering canine dimorphism. *Am. J. Phys. Anthropol. Supp.* 16:159.
- Plavcan JM, van Schaik CP, and Kappeler PM (1995) Competition, coalitions and canine size in primates. *J. Hum. Evol.* 28:245–276.
- Smith RJ (1981) Interspecific scaling of maxillary canine size and shape in female primates: Relationships to social structure and diet. *J. Hum. Evol.* 10:165–173.